3. *A suggested clarification of the Taxonomic Status of the South African Titanosuchians.*

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(With Plates I–IX)

Introduction

Being engaged on a morphological study of the Deinocephalians the need has arisen to establish some order in the systematics of the group. In an assessment of the importance of the various morphological features the existence of a number of generic and specific names, not associated with at least some of the main morphological characters, is merely confusing and an encumbrance.

In the literature there are about half a dozen generic and a somewhat greater number of specific names that signify next to nothing. One is led to wonder why they were ever created at all. One realizes that due to the nature of the material dealt with in palaeontology, it is not always possible to describe only relatively well-preserved specimens. There is some justification, although one doubts the wisdom, if a newly discovered fragment establishes the existence of a group hitherto unknown to science (as, for instance, Owen's creation of *Titanosuchus ferox*), but there is no justification for subsequent authors to create additional names for specimens that do little more than prove that there are more individuals of the group besides the original individual. It is, of course, fully realized that the vertebrate palaeontologist generally deals with individuals and that his species mostly refer to single individuals and are hardly ever the norm of a good series.

In the Titanosuchians sixteen generic names have been created up to date. Of these only five (*Jonkeria*, *Dinosphageus*, *Anteosaurus*, *Dinophoneus*, and *Dinosuchus*) are based on reasonably fully preserved skulls, one (*Phoneosuchus*) on a good lower jaw, and the other ten (*Titanosuchus*, *Archaeosuchus*, *Dinartamus*, *Scapanodon*, *Lamiasaurus*, *Dinocynodon*, *Enobius*, *Scullya*, *Dinopolus*, and *Titanognathus*) are all based on either skull fragments or parts of dentaries.

In two former papers, in 1935 and 1936, I have shown that two of the above names must fall away—*Dinophoneus* and *Phoneosuchus* being both synonyms of *Jonkeria*. In the sequel a further reduction of generic names will be proposed.

At this stage I am only considering the cranial material on which, in any case, the authors have mainly created their new genera and species. I have critically examined most of the described specimens and for the rest have extracted the pertinent points from the descriptions of the authors concerned. In addition there is at the South African Museum a large collection, mainly collected by myself in recent years, of undescribed material which includes a dozen or so really good skulls. I now wish to present tentatively, for criticism by colleagues, a solution of the taxonomic maze formed by the plethora of names. With due

regard to the fetish of the law of priority I have attempted to include as many of the fragmentary specimens as is possible instead of simply regarding them as generically or specifically indeterminate.

Sex and Age in the Titanosuchians

In addition to the fragmentary nature of many of the types there are other difficulties in arriving at a reasonable classification. With the small number of individuals known we have little to indicate sex in the Titanosuchians. It must, however, be kept in mind that a smaller size, lighter build and a lesser degree of pachyostosis, particularly with regard to bosses, may indicate the female of the species.

Without a reasonably long series of specimens it is difficult to determine the effects of age in the Titanosuchian skull. In the Tapinocephalian, *Moschops*, Gregory found an increasing pachyostosis, especially of the postorbital bar, a character indicating increasing age. In some of the Titanosuchians, especially of the *Anteosaurus* group, there is a slight variation in the thickening of the postorbital bar, but whether this is due to age or sex is uncertain. In the *Jonkeria* group there are marked differences in size unaccompanied by other differences of generic value. Here size is not considered a character of generic value and at most may be regarded as specific, but in some cases may very well be a character of full maturity. Thus *Dinosphageus* is considered to be a large species of *Jonkeria*, but may very well prove to be a fully grown specimen of one of the previously described species of *Jonkeria*. The strength and size of the dentary, particularly of the mentum, have been used as a character of systematic value, but is it not probable that a moderately strong dentary with a sloping mentum may become massive with a fairly upright mentum with increasing age? This was one reason for regarding the name *Enobius* as unnecessary.

The Dentition

The dentition of the Deinocephalians presents some very interesting conditions. A detailed study of the modifications and their implications should be undertaken. Here I can only touch on some aspects. A study of the teeth is made very difficult because of the poor preservation in most specimens. In the majority of cases the crowns are not preserved and we are forced to study stumps and cross-sections at varying levels which are not directly comparable. The presence of a lingual crushing surface internal to a talon in many teeth very materially affects the nature of the cross-section at different levels. Where crowns are preserved the intractable nature of the matrix of the *Tapinocephalus* zone makes it difficult to free them from the matrix satisfactorily.

The Titanosuchians have a heterodont dentition with incisors, canine and postcanines. In some forms the incisors are fairly short with a labial talon and a lingual crushing surface, in others the incisors are long to very long with a talon long to very long and the lingual crushing surface is poorly developed or represented only by a cingulum, or wholly absent. The canines are strong to

very strong, simple, pointed teeth of a typical carnivorous nature with, in some cases, a possibly serrated posterior cutting edge. What little is known of the postcanines indicates a considerable variation in the nature of the crowns—some have flattened crowns with serrations, others short or longish conical teeth.

Now, is the heterodont Titanosuchian dentition to be morphologically derived from the homodont dentition of the Tapinocephalians? The Tapinocephalian teeth all have a talon, pointed or somewhat flattened, and a lingual crushing surface varying in strength, from which the different Titanosuchian types of teeth could be morphologically derived. The medium-sized incisors of a form like *Jonkeria*, with its short talon and definite lingual crushing surface, would then represent a more primitive stage than the long incisors of some of the Anteosaurians which are all talon with no crushing surface. The stages in this transition could then be used for taxonomic purposes. But, in *Dinartamus*, Broom found a mixture of these two types of incisors and the question arises whether this may not represent a difference in the consecutive sets of incisors. We do not know how many times the Titanosuchians replaced their incisors. Hitherto only two sets have been described. On this subject the external nature of the teeth gives little information and we have to rely on fortuitous weathering and fracturing or sectioning. The material at my disposal affords no evidence as to whether the Jonkerian type of incisor is the deciduous type and the Anteosaurian type typical of a later set of teeth. Until we have evidence supporting Broom's observations on *Dinartamus* I propose to consider the presence or absence of the lingual crushing surface in the incisors to be a specific character present in the consecutive sets of teeth, and not dependent on age.

Besides having these two types of incisors the Titanosuchians also possess a variable number of incisors—as described, from 0 to 5. In those specimens where the premaxilla is edentulous the condition can be interpreted in a number of ways: the incisors may have been shed postmortemly, or being juvenile they have not yet erupted, or being gerontic they have been lost. The nature of the material being what it is, it is difficult to decide which explanation best fits each case. Sectioning through the alveolar region is not always possible in order to base a count on the nature of the alveoli. The usual number of incisors is 5 but in some forms it is 4 or even 3. Can the number be considered a character of systematic value? If the juvenile and mature incisors are of the same size then obviously the premaxilla of a young animal could only house a smaller number than that of the mature animal. In using the number of incisor teeth as a taxonomic character the age of the animal must thus be taken into account.

The number of postcanine teeth in the Titanosuchians varies greatly, from 1 to 19, and is of doubtful systematic value. In some, these teeth are small; in others, strong; in some specimens they are regularly spaced and in others quite irregular. The two sides are often dissimilar, e.g. in *Enobius* there are, according to Broom, in the left dentary '. . . portions of three molars. There certainly have been four, and very probably there have been five', and on the right side

Broom found only one tooth behind the canine. In general it can be stated that in the Jonkerias the postcanines are regularly spaced and form a long series, whereas in the Anteosaurians they are irregular and the series is short.

With the material at my disposal I can state that the dentary usually has one incisor less than the corresponding premaxilla. It would also appear that there are fewer postcanines in the dentary than in the opposing maxilla.

Teeth on the palatines occur in the Anteosaurians and in the fragment called *Scullya*, but have as yet not been recorded in the Jonkerias although I found some indication in *Jonkeria ingens* (A.M.N.H. No. 5608).* These teeth are mostly seen only in section but in S.A.M. No. 11592 there is preserved a small pointed tooth slightly recurved. In the Anteosaurians the palatine teeth are situated on a prominent elevation, semilunar or reniform in shape. Their function seems clear—the incisors and canines tear out a lump of flesh from the victim and this is then held by the raised palatine teeth as an intermediate stage in the swallowing process. The palatine teeth situated on this characteristic boss constitute a diagnostic character of value.

Key for the Genera

Bearing the above remarks in mind we may now proceed with our attempt to arrange the Titanosuchians in some reasonable order. As a preliminary step, and in practice of considerable value, to facilitate the process of a rough-and-ready sorting out of the 14 genera, I propose making use of the following key:

A. Forms without bosses on postorbital bar and angular, incisors not long and with step:
   1. With many regular postcanines, no palatine boss—*Jonkeria*, *Dinosphageus*, *Dinopolus*.
   2. With few postcanines—*Dinartamus*.

B. Forms with bosses on postorbital bar and angular, incisors long and without step:
   3. With variable irregular postcanines, prominent palatine boss—*Anteosaurus*, *Dinosuchus*.
   4. With variable irregular postcanines, probably with palatine boss—*Titanosuchus*, *Scapanodon*, *Archeosuchus*, *Lamiasaurus* (snout), *Dinocynodon*, *Scullya*, *Titanognathus*, *Enobius*.

Redefinition of Genera

With our increased knowledge of the Titanosuchians it has become advisable to redefine the valid genera:

* For the institutions housing the specimens here referred to the following abbreviations are used: A.M.N.H., American Museum of Natural History, New York. S.A.M., South African Museum, Cape Town. B.M., British Museum (Natural History), London. T.M., Transvaal Museum, Pretoria. A.K., Alte Akademie, Munich. K.M., Kimberley Museum, Kimberley.

I. *Jonkeria* van Hoepen 1916.

The genotype *J. truculenta* is based upon an excellent skull and lower jaw.

1. Skull size—this is medium to large, not massive.
2. Bosses—there are no prominent bosses.
3. Additional pachyostosis—the parietals form a prominent ridge thickened round the pineal foramen but do not form a well-demarcated boss.
4. Palatine—there is no prominent boss, but the palatine is possibly dentigerous.
5. Premaxilla—the dentigerous border does not curve upwards and there is also no corresponding upward sweep of the dentary.
6. Incisors—are of medium length with labial talon pointed and with well-developed lingual crushing surface.
7. Pineal foramen—penetrates anterior part of the parietals and is thus some distance from the occipital border.
8. Snout—is relatively long, broader than high, the frontals are only slightly swollen, the premaxilla is fairly flat.
9. Squamosal—does not extend far ventrally and does not sweep far posteriorly, posterior to the interparietal. There is also little lateral sweep of the squamosal.
10. Temporal fossa—this is fairly large, with the antero-posterior and dorso-ventral diameters moderate and approximately equal, not extending much laterally, as the squamosal does not sweep much outwards.
11. Intertemporal width—this is small to moderate; the parietals are laterally pinched in to form a fairly high and narrow parietal crest.
12. Dentary—this is strong but not massive, with sloping mentum.
13. Dental formula—$i.\frac{4-5}{4}$, $c.\frac{1}{1}$, $p.c\ \frac{14-19}{13-15+}$.

Synonym. As thus defined *Dinosphageus* and *Dinopolus* become congeneric with *Jonkeria*.

II. *Anteosaurus* Watson 1921.

The genotype, *A. magnificus*, is based upon the major portion of a skull somewhat weathered.

1. Skull size—this is small to very large, slightly to very massive.
2. Bosses—a medium to very prominent boss is present on the dorsal part of the postorbital bar, and there is a prominent oval boss on the angular, the boss on the jugal is absent or low and moundlike to very prominent.
3. Additional pachyostosis—the parietals are much thickened but do not form a crest, greatly thickened around the pineal foramen to form a mound or well-demarcated circular boss; the frontals are greatly thickened to produce a medium to very prominent swelling.

4. Palatine—there is a prominent semilunar ridge-like or reniform boss-like eminence carrying irregular small pointed teeth.
5. Premaxilla—the dentigerous border curves antero-dorsally to form an obtuse angle with the maxillary border and there is little corresponding upward sweep of the anterior part of the dentary.
6. Incisors—are long to very long, the labial talon forming most or all of the tooth, with the lingual crushing surface greatly reduced to form little more than a cingulum, or are altogether absent.
7. Pineal foramen—penetrates the posterior part of the parietals and is thus near the occipital border.
8. Snout—is of medium length, higher than broad, the frontals are greatly swollen, the premaxilla is dorsally swollen and demarcated from the maxilla by a groove.
9. Squamosal—extends moderately to far ventrally and sweeps far posteriorly, i.e. much posterior to the occipital surface of the interparietal, and sweeps far to very far outwards.
10. Temporal fossa—this is large, with the dorso-ventral diameter greater than the antero-posterior, extending much laterally due to the outward sweep of the squamosal.
11. Intertemporal width—this is moderate to large, the parietals are laterally somewhat pinched in, but do not form a high and narrow crest.
12. Dentary—this is strong and fairly to very massive, with fairly upright mentum.
13. Dental formula—i.$\frac{3-5}{3-4}$, c.$\frac{1}{1}$, p.c.$\frac{5-15?}{5-?}$

Synonyms. As thus defined *Dinosuchus* becomes congeneric with *Anteosaurus*.

III. *Dinartamus* Broom 1923.

The genotype, *D. vanderbyli*, is based upon portions of a skull, probably associated.

1. Skull size—this is probably large, not massive.
2. Bosses—no evidence is preserved.
3. Additional pachyostosis—no evidence of this is preserved.
4. Palatine—no evidence of a palatine boss is preserved.
5. Premaxilla—the border does not curve upwards.
6. Incisors—according to Broom, 'the first is of Deinocephalian type, but the other three incisors may have had pointed crowns. There is some little indication that this may have been so.'
7. Pineal foramen—this area is not preserved.
8. Snout—this is weathered.
9. Squamosal—this is not preserved.
10. Temporal fossa—this region is not preserved.
11. Intertemporal width—this region is not preserved.

12. Dentary—in the associated specimen the dentary is apparently fairly massive with a fairly upright mentum.
13. Dental formula—according to Broom, i.$\frac{4}{3}$, c.$\frac{1}{1}$, p.c.$\frac{5}{5}$.

IV. *Titanosuchus* Owen 1879.

The genotype, *T. ferox*, is based upon upper and lower jaw fragments showing sections of the teeth roots. The only diagnostic features that can be determined in the genotype are: dentary strong and massive with mentum apparently fairly upright, and dental formula: i.$\frac{5}{4}$, c.$\frac{1}{1}$, p.c.$\frac{11}{10\text{-}11}$.

Other forms considered here are:

Titanosuchus cloetei (Broom 1903) is based on a piece of massive dentary, with the incisors lacking a lingual crushing surface and with the dental formula: i. 4, c. 1, p.c. 4+.

Scapanodon (Broom 1904). The type species is based upon two imperfect, badly preserved jaws showing a series of teeth: i. 2+, c. 1, p.c. 11+.

Archaeosuchus (Broom 1905). The type of the type species is a partial maxilla with some teeth; according to Broom c. 1, p.c. 8 (in 1932 Broom gives 7 postcanines).

Lamiasaurus (Watson 1914). Only the snout is considered here. The premaxillary border is not dorsally directed and the dental formula is i. 4 or 5, c. 1, p.c. 3–4.

Dinocynodon (Broom 1929). For the type dentary Haughton (1915) states that the symphysis is massive and square, and the dental formula is i. 4, c. 1, p.c. 11+, and Broom gives as the only generic character 'the extreme flattening of the large canine'. Now, in a specimen of *Anteosaurus*, there is a canine on the point of being shed which is also flattened, and this character can thus hardly be considered of generic value.

Scullya (Broom 1929). The type species is based upon 'a very badly crushed snout' with the dental formula i. 5, c. 1, p.c. 12, and the only other characters are the possible presence of teeth on the palatine and the dentary massive.

Titanognathus (Broili and Schröder 1935). The type of the type species consists of skull fragments showing, 'Schädel mit schmaler und steil vom prämaxillaren Kieferrand aufsteigender Schnauze, sehr gross. Praemaxillarer Kieferrand gegenüber dem maxillarer stark in die Höhe gezogen, Symphysenregion des Unterkiefers entsprechend erhöht gegenüber dem rückwartigen Abschnitt des Dentale. Zahnformel: i. $\frac{5}{4(?)}$ c. $\frac{1}{1}$, p.c. $\frac{6}{+3?}$'.

Enobius (Broom 1923). The type of the type species consists of two dentaries; mentum massive and squarish, with the dental formula c. 1, p.c. 1–5.

From the above it is quite evident that this series of fragmentary 'types' affords no very trustworthy bases on which they can be distinguished from

each other generically. I propose lumping all these forms together and to redefine the genus *Titanosuchus* compositely as follows:

1. Skull size—this is very probably large and massive.
2. Bosses—are probably present.
3. Additional pachyostosis—of this no evidence is preserved.
4. Palatine—this is not preserved.
5. Premaxilla—the dentigerous border curves antero-dorsally with an associated step-up of the anterior part of the alveolar border of the dentary.
6. Incisors—these are apparently long, with no lingual crushing surface.
7. Pineal foramen—no evidence is preserved.
8. Snout—is probably as in *Anteosaurus*.
9. Squamosal—is not preserved.
10. Temporal fossa—this area is unknown.
11. Intertemporal width—this area is not preserved.
12. Dentary—this is strong and massive with a squarish and upright mentum.
13. Dental formula: i. $\frac{4-5}{4}$, c. $\frac{1}{1}$, p.c. $\frac{11-15+}{7-12+}$.

Synonyms: *Scapanodon*, *Archaeosuchus*, *Lamiasaurus* (snout), *Dinocynodon*, *Scullya*, *Enobius*, and *Titanognathus*.

The Specific Names of the Above Forms

Until a detailed study is completed it is impossible to make any statement on the validity of the specific names given by authors. Meanwhile a list is appended of the names as they stand at the present moment in the literature, but under the genera—*Anteosaurus*, *Dinartamus*, *Jonkeria* and *Titanosuchus*—as defined above.

Genus *Anteosaurus*:

A. abeli Boonstra 1952. Plates I–V and IX.
Type. A good skull and lower jaw. S.A.M. No. 11296.

A. magnificus Watson 1921.
Type. Major part of skull. B.M. No. 3595.

A. minor (Broom) 1929.
Type. Fragment of skull. B.M. No. 5742.
Referred specimens:
S.A.M. No. 11492. A somewhat weathered skull.
S.A.M. No. 11694. A good skull. (Plate VI, figs. 1, 2.)
Additional diagnostic features revealed by these two skulls are: In S.A.M. No. 11492, the left premaxilla has no incisors preserved, but on the right side there are three incisors, fairly long, with no indication of a lingual step; in S.A.M. No. 11694 no incisors are present, the dentigerous boss on the palatine is prominent and semilunar in outline; there is no indication of a jugal boss. The dental formula is i. 0–3, c. 1, p.c. 7–8.

A. vorsteri (Broom) 1936.
Type. A good skull. T.M. 265, Broom's *Dinosuchus vorsteri.*
Referred specimen: a good skull. S.A.M. No. 11577. (Plates VII and VIII.)

Genus *Dinartamus:*

D. vanderbyli Broom 1923.
Type. Skull fragments. Coll. Broom.

Genus *Jonkeria:*

J. angusticeps (Broom) 1929.
Type. Good lower jaw. A.M.N.H. No. 5633. Broom's *Phoneosuchus angusticeps.*

J. haughtoni (Broom) 1939.
Type. Fairly good skull. S.A.M. No. 4343. Broom's *Dinosphageus haughtoni.*

J. ingens (Broom) 1923.
Type. Fair skull. A.M.N.H. No. 5634. Broom's *Dinophoneus ingens.*
Synonym. *J. pugnax* (Broom) 1929. Fairly good skull and lower jaw. A.M.N.H. No. 5608.

J. truculenta van Hoepen 1916.
Type. Good skull and lower jaw. T.M. 212.

J. vanderbyli (Broom) 1929.
Type. Good skull. A.M.N.H. No. 5620.

J. spp. The lack of identifiable cranial elements makes the specific status of *J. crassus* (Broom) 1929, Type A.M.N.H. No. 5577, uncertain. The skull referred to *Scapanodon duplessisi* by Broom 1923 is undoubtedly a *Jonkeria* species. Further study may prove synonomy with one of the named species and until then it is best left unnamed. *Dinopolus atrox* Broom 1923, Type T.M. 274, consists of a snout. The incisors are short, the anterior three with ledge, the outer without ledge, according to Broom. The lower canine peculiar, but otherwise it falls under *Jonkeria* as here defined. These characters may indicate that it is a distinct species—*Jonkeria atrox* Broom, bridging the gap between *Dinartamus* and *Jonkeria.*

Genus *Titanosuchus:*

T. cloetei (Broom) 1903.
Type. Piece of dentary. S.A.M. No. 731.

T. dubius (Haughton) 1915.
Type. Major part of dentaries. S.A.M. No. 2759. Broom's *Dinocynodon dubius.*

T. ferox Owen 1879.
Type. Upper and lower jaw fragments. B.M. No. 49370.

T. gigas (Broom) 1929.
Type. A very badly crushed snout. Coll. Broom. Broom's *Scullya gigas.*

T. lotzi (Broili and Schröder) 1936.

Type. Skull fragments. A.K. (no number given). Broili and Schröder's *Titanognathus lotzi*.

T. strubeni (Broom) 1923.

Type. Partial dentaries. K.M. (no number given). Broom's *Enobius strubeni*.

Incertae sedis. The following forms do not merit separate generic rank and may best be regarded as species of *Titanosuchus*, whose specific validity is questionable.

T. duplessisi (Broom) 1904.

Type. Imperfect badly preserved jaws. S.A.M. No. 769. Broom's *Scapanodon duplessisi*.

T. cairncrossi (Broom) 1905.

Type. Part of maxilla. S.A.M. No. 916. Broom's *Archaeosuchus cairncrossi*.

T. newtoni (Watson) 1914.

Type. Snout. B.M. No. 49385. Watson's *Lamiasaurus newtoni*.

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